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Chasmaporthetes kani, New Species from China, With Remarks on Phylogenetic Relationships of Genera within the Hyaenidae (Mammalia, Carnivora)

HENRY GALIANO[1] AND DAVID FRAILEY[2]

ABSTRACT

A new species of *Chasmaporthetes* is described from deposits of Early Pleistocene age in Shansi Province, People's Republic of China. The concept of *Chasmaporthetes* is extended to include "*Lycyaena*" ("*Euryboas*") *lunensis* Del Campana, 1914 but not *Euryboas bielawskyi* Schaub, 1941. Within a cladistic framework, *Chasmaporthetes* is the sister group of *Euryboas*; *Chasmaporthetes*, *Euryboas*, and *Lycyaena* form the sister group of *Hyaenictitherium*, *Hyaena*, *Pachycrocuta*, and *Crocuta*.

INTRODUCTION

The first description of a hyaenid in the New World was that of *Chasmaporthetes ossifragus* by Hay (1921) from the Anita Fauna (Irvingtonian), Coconino County, Arizona. Stirton and Christian (1940) described a second genus and species *Ailureana johnstoni*, from North Cita Canyon (late Blancan), Randall County, Texas, which they later (1941) transferred to *Chasmaporthetes*. *Chasmaporthetes ossifragus* has been recorded in two Florida faunas: Santa Fe River 1B, Blancan (Webb, 1974) and Inglis 1A, Irvingtonian (Klein, 1971; Webb, 1974). Undescribed or poorly preserved material that possibly are hyaenids have been mentioned from early Blancan localities in Kansas (Hibbard, 1950); Idaho (Bjork, 1970); Arizona and Mexico (Repenning, 1962).

The material discussed in the present paper was assembled by the late Childs Frick between 1931 and 1939. At the conclusion of the Central Asiatic Expeditions of the American Museum of Natural History, Liu Hsi Ku and Kan Chuen-pao ("Buckshot") were employed by Frick to continue field collection in Late Tertiary and Quaternary deposits of China. The efforts of these men produced an extensive collection of Late Cenozoic fossils from numerous localities, three of which yielded specimens of an Asiatic representative of the genus *Chasmaporthetes*. This sample of *Chasmaporthetes* from China and the additions to the North American hypodigm have served to clarify the phyletic position of *Chasmaporthetes* within the Hyaenidae.

The age of the Chinese deposits was determined by the fauna associated with *Chasmaporthetes kani*. Complete faunal lists of the Frick China localities and the justification (or modifi-

[1]Curatorial Assistant, Department of Vertebrate Paleontology, the American Museum of Natural History, New York, 10024.

[2]Student, Department of Systematics and Zoology and Museum of Natural History, University of Kansas, Lawrence, 66045.

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cation) of this age assignment are in preparation by Tedford, Manning, and Galiano.

The authorship of this paper is about equally divided. The senior author was responsible for the general outline and the discussions of generic affinities and ecological relationships. The junior author organized the paper and was responsible for the description and discussion of *Chasmaporthetes.*

All measurements are in millimeters. Parentheses indicate an approximate measurement. Abbreviations used are:

AMNH, the American Museum of Natural History
F:AM, Frick Collection, the American Museum of Natural History
QSV, Museum de Lyon, France
TRO, Timberlane Research Organization, Lake Wales, Florida
UF, University of Florida, Gainesville, Florida
USNM, National Museum of Natural History, Smithsonian Institution.

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SYSTEMATICS

ORDER CARNIVORA BOWDICH, 1821

SUBORDER AELUROIDEA FLOWER, 1869

CHASMAPORTHETES HAY, 1921

Type species. Chasmaporthetes ossifragus Hay, 1921.

Included species. Chasmaporthetes johnstoni (Stirton and Christian, 1940). *C. lunensis* (Del Campana, 1914); *C. borissiaki* (Khomenko, 1932); *C. kani*, new species; ? *C. nitidula* (Ewer, 1955).

Revised Generic Diagnosis. P^1 larger than in other hyaenid genera (absent in *Euryboas*). Anterior accessory cusps of P_2^2 and P_3^3 more prominent than in other hyaenids; upper and lower tooth rows curved with premolars slightly imbricate, as opposed to a straight tooth row as in *Euryboas.*

Chasmaporthetes kani, new species

Holotype. F:AM 99789, palate, with nearly complete dentition missing only the left P^1 (lost in life).

Type Locality. Hsia-chuang, approximately 20 km. south of Shou Yang, Shou-yang District, Shansi Province, People's Republic of China.

Age. Nihowanian (Early Pleistocene).

Etymology. Named for Kan Chuen-pao, member of the Central Asiatic Expeditions and professional fossil collector for the Frick Laboratory.

Diagnosis. M_1 slightly longer than P_4; anterior accessory cusps of P_2 and P_3 relatively weak as compared with other *Chasmaporthetes* species.

Hypodigm. Hsia-chuang: F:AM 99784, palate with right I^{1-3}, C^1, P^1-M^1, left I^{1-3}, C^1, P^1; F:AM 99785, left ramus with C_1, P_2-M_1 (P_4 broken); F:AM 99786, left ramus with C_1, P_2-M_1; F:AM 99787, right ramus with 1_3, C_1, P_2-M_1; F:AM 99788, left ramus with C_1 (broken), P_2-M_1. Ma Tzu Kou: F:AM 99781, right ramus with I_{1-3}, C_1, P_2-M_1; F:AM 99790, left ramus fragment with M_1. Niu Wa Kou: F:AM 99783, partial skull with right I^{1-3}, C^1, P^1-M^1, left I^{1-3}, M^1; F:AM 99782, immature left ramus with I_1, DI_{2-3}, DC_1, DP_{2-4}. Ma Tzu Kou and Niu Wa Kou are in Yu-she District, Shansi Province.

A check was made to determine if any two specimens of the hypodigm belong to the same individual. This did not prove to be the case.

Material Used for Comparison. Chasmaporthetes ossifragus. AMNH 99098 (cast of holotype, USNM V-10023), edentulous ramus, from the Val Verde Mine near Anita, Coconino County, Arizona; AMNH 95208, left ramus with P_2-M_1 (cast of UF 18088), from Inglis 1A, Citrus County, Florida; AMNH 100078 (cast of TRO SF-1) left detached P^2, Santa Fe River, Florida (courtesy of John Waldrop); F:AM 23390, fragmentary left ramus with P_{2-4}, from Benson area, Cochise County, Arizona. *Chasmaporthetes johnstoni*: Panhandle Plains Museum no. 2343, holotype left ramus with I_3, C_1, P_2-M_1, text and figures in Stirton and Christian (1940), from Randall County, Texas. *Chasmaporthetes lunensis*: partial skull with upper dentition, text and figures in Del Campana, 1914, from Olivola (Val di Magra), Italy. *Euryboas bielawskyi*: AMNH 101261 (cast of unnumbered holotype housed in Falculté des Sciences, Clermont-Ferrand, France), mandible with complete dentition from Rocca Neyra, Montagné de Perrier, France; AMNH 99148 (cast of Mus. Basel, V.A. 1822), maxillary fragment with P^{3-4} from Val d'Arno, Italy; *Euryboas* sp.: AMNH 26995 (cast of QSV 53), anterior portion of a skull with nearly complete dentition missing right I^{1-2}, and left I^{1-3}, C^1, from St. Vallier, France.

DESCRIPTION

Skull. Neither the skull roof nor the portion of the skull posterior to the glenoid fossa is preserved in the Chinese sample. The remaining part of the skull is comparable in size to the corresponding elements in *Crocuta crocuta.*

The postorbital processes are small and blunt as in *Palhyaena* and *Lycyaena.* In *Hyaena* and *Crocuta* these processes are more prominent. The area behind the postorbital process is not so constricted as in *Crocuta*, but slightly swollen, as in *Lycyaena.* The forehead is domed and joins the muzzle immediately posterior to P^3. The muzzle is high and flattened dorsally, giving a much sturdier appearance to the snout than that of *Crocuta crocuta* (see fig. 2).

The anterior opening of the infraorbital foramen lies above the parastyle of P^4. This condition is seen in many hyaenids but altered in *Hyaena*, *Pachycrocuta*, and *Crocuta* in which the opening of the infraorbital foramen lies above P^3. A thumbprint-sized depression is present in the zygomatic arch just ventral to the orbit at the place the dorsal portion of the buccinator muscle takes its origin. This depression is present in *Euryboas* but not in available specimens of *Crocuta crocuta.*

The anterior margin of the braincase rises at approximately a 75 degree angle from the glenoid fossa leaving a large, deep temporal fossa behind the orbit. This condition also exists in all advanced hyaenid genera with some slight variation.

The alignment of the foramen rotundum, anterior lacerate foramen, and the optic foramen parallels the anterior margin of the braincase, placing these foramina in a vertically compact group in which neither the optic foramen (anteriorly) nor the foramen rotundum (posteriorly) extends anterior to the margin of the anterior lacerate foramen.

Ventral to the orbit, the area of origin for the anterior part of the medial pterygoid muscle slopes smoothly to the posterior margin of the palate with no evident sculpture for the attachment of this muscle.

The posterior and anterior widths of the palates vary, due perhaps to sexual dimorphism. The width of the palate between the canines may be less than the length of P^4 (in F:AM 99784) or may be greater than the length of P^4 (F:AM 99789, see measurements in table 1). In a similar fashion, the posterior width of F:AM 99789 is greater than the length of the upper tooth row (C^1-P^4), whereas in F:AM 99784 it is less. F:AM 99783, which is more like F:AM 99784 in robustness of canines and premolars, is intermediate in both cases. The palatal proportions described above, in *Euryboas* (QSV 53) are like those of F:AM 99789 (see fig. 1).

Dentition. The upper tooth row is slightly curved between P^2 and P^4, not to the degree in *Crocuta*, but more than that of *Euryboas*. C^1 and P^1 lie parallel to the long axis of the skull producing a change in the curvature of the tooth row at this point. P^2, and to a lesser extent P^3, are slightly rotated medially in F:AM 99783 and 99789; but in F:AM 99784, P^3 shows the greater rotation. This rotation of premolars, with imbrication, increases the illusion of curvature in the tooth row.

TABLE 1

Measurements (in Millimeters) of *Chasmaporthetes kani*

(Approximate measurements are in parentheses.)

Palates and Upper Dentitions	F:AM 99783	99784	99789 (holotype)
Length of upper tooth row, C^1-P^4, measured at gumline	92.5	98.1	100.4
Width of palate, measured at widest points on P^4s	96.5	87.6	104.4
Width of palate, measured between lingual alveolar borders of canines	33.9	27.9	(37)
Length X width			
I^1	6.0 X 5.0	6.3 X 4.7	7.2 X 5.3
I^2	6.8 X 5.5	7.1 X 5.9	7.5 X 6.2
I^3	10.0 X 7.6	9.2 X 7.7	10.3 X 8.0
C^1	14.2 X 10.6	13.8 X 11.5	16.0 X 13.7
P^1	8.2 X 7.4	8.7 X 7.7	9.5 X 8.4
P^2	19.3 X 11.7	16.6 X 10.7	18.4 X 11.5
P^3, length X width	21.4 X 13.4	21.3 X 13.6	22.9 X 14.2
P^4, length, parastyle to metastyle	33.2	31.4	33.3
P^4, length, protocone to metastyle	33.6	32.0	34.8
P^4, width, protocone to parastyle	17.7	17.3	18.9
M^1, length X width	7.7 X 16.1	7.2 X 15.2	7.8 X 17.8

Rami and lower dentitions	F:AM 99781	99785	99786	99787	99788	99790
Length, from anterior edge of incisors to posterior edge of condyle	–	–	–	191.5	–	–
Length, of tooth row, P_2-M_1, measured at gumline	79.0	78.0	82.5	(78.5)	82.4	–
Depth of mandible between C_1 and P_2 (symphysis)	34.5	37.0	43.4	40.1	41.9	–
Greatest depth of mandible below M_1	(36.1)	36.9	–	39.8	42.6	36.3
Length X width						
C_1	13.9 X 10.4	15.1 X 11.2	16.5 X (13)	–	–	–
P_2	15.8 X 8.1	15.0 X 8.7	16.6 X 9.6	(14.6 X 8.6)	17.2 X 10.2	–
P_3	18.9 X 9.8	18.5 X 10.0	19.5 X 11.5	18.3 X 10.3	20.8 X 11.8	–
P_4	22.4 X 10.3	(21.3) X 10.9	22.8 X 12.7	22.1 X (12.5)	22.8 X 12.4	–
M_1	23.8 X 9.3	24.7 X 11.2	26.8 X 12.8	(23.8) X 11.4	26.5 X 12.3	23.7 X 9.8

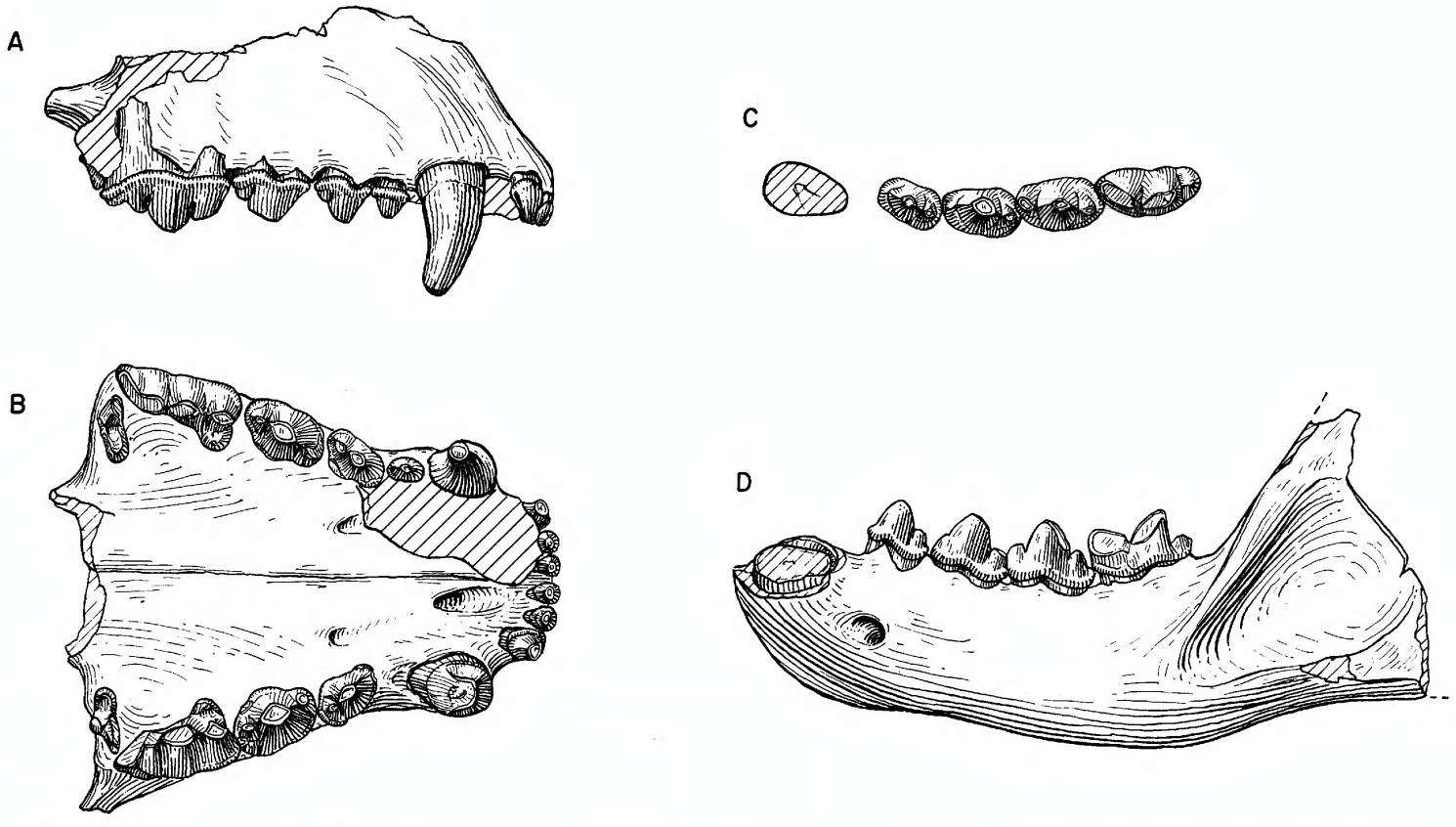

FIG. 1. *Chasmaporthetes kani.* A, B, Type. F:AM 99789; A. Lateral view. B. Palatal view. C, D, F:AM 99788; C. Occlusal view. D. Lateral view. All figures × 1/2.

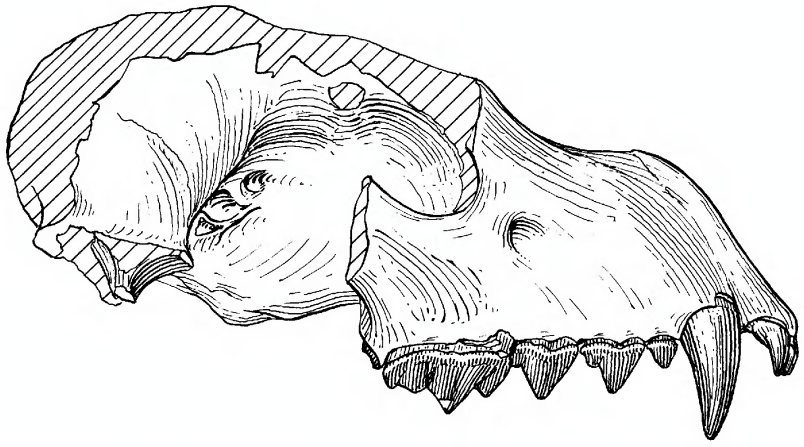

FIG. 2. *Chasmaporthetes kani*, new species F:AM 99783, lateral view, × 1/2.

The incisors are proportioned as those of *Palhyaena* or *Lycyaena*. I^1 and I^2 are subequal in size; I^2 is the larger. I^{1-3} have faint anterior cingula. I^1 and I^2 have large posterior cingula; that of I^3 is barely noticeable.

C^1 is of normal hyaenid shape with two small ridges, one anteromedial and one posterior, running the length of the crown.

All the cheek teeth have faint labial and lingual cingula, as in all members of the hyaenidae.

P^1, absent in *Euryboas*, is proportionally larger than in any other hyaenid genus. The imbrication of P^2 and P^3, as described above, may be the result of accommodating this unusually large tooth. P^1 is about half the length of P^2, essentially unicuspid, has a convex labial surface, and a concave lingual surface. P^1 of F:AM 99784 has very distinct anterior and posterior accessory cusps.

P^2 and P^3 have more prominent anterior accessory cusps than those in *Euryboas*, although that of P^2 may not be clearly evident. The posterolingual margins of P^2 and P^3 are broadly expanded, creating a lingual shelf on these teeth.

P^4 has a protocone that is round in occlusal outline, which does not reach to the anterior margin of the tooth. In contrast to *Euryboas*, the protocone does extend to the anterior margin of the tooth. The tip of the paracone is at the approximate center of the tooth. The parastyle is larger than in *Euryboas*, comprising slightly over one-quarter of the length of P^4.

M^1, as in *Euryboas*, has one lingual cusp and one or two labial cusps separated by a basin which occludes with the single-cuspid talonid of M_1.

The lower jaws are reminiscent of the type of *E. bielawskyi*, in shape and size. The ramus has a deep, upright symphyseal region that extends below the natural curve of the ramus producing a doubly curved ventral margin, i.e., the margin is convex beneath the canine as well as beneath the carnassial. A single large mental foramen is placed beneath the anterior root of P_2. The masseteric fossa is moderately deep, the indistinct anterior border of the masseteric fossa is beneath the talonid of M_1. The angular process, the area of insertion for the medial pterygoid muscle, is rounded and does not extend posteriorly to the condyle. This corresponds to the poor demarcation on the skull of the origin of the anterior portion of the medial pterygoid muscle as discussed previously. The mandibular foramen is placed about midway on a line between the talonid of M_1 and the angle of the ramus. Like the mental foramen, the mandibular foramen is large.

The lower incisors are proportioned as those of *Lycyaena* and *Euryboas*. I_1 and I_2 are small and subequal in size, I_2 is larger. I_3 has a small posteroexternal accessory cusp. The lower canine has weak anterior and posterior ridges running the length of the crown.

P_1 is absent, as in all *Chasmaporthetes* and *Euryboas* species examined except for the curious exception of *C. borissiaki*, where this tooth is

present only on the right side of the mandible. The presence of P_1 is variable in *Lycyaena.*

The lower cheek teeth become progressively larger from P_2 to M_1. Each has a faint cingulum around the base of the crown. On P_3 and P_4 this cingulum may be enlarged lingually to the posterior accessory cusp, as in other species of *Chasmaporthetes* and *Euryboas*. As in other *Chasmaporthetes* species, the premolars are tricuspid, the cusps are placed on the long axis of each tooth. The size of the anterior accessory cusp on P_{2-4} is also variable. It may be barely discernible on P_2 and small but evident on P_3, or small on P_2 and clearly evident on P_3. In either case, the anterior and posterior accessory cusps are of equivalent size on P_4.

The variation in prominence of the anterior accessory cusps on P_2 and P_3 is possibly related to sexual dimorphism as those rami in which the anterior accessory cusps of P_2 and P_3 are most prominent also have the more robust premolars and canines. Generally, P_2 to P_4 are oval in outline although in several individuals, again probably due to sexual dimorphism, the lower premolar widens posteriorly. Unfortunately, as no other population samples of *Chasmaporthetes* are known, comparison of these features is impossible.

The length of the largest M_1 (F:AM 99788) is greater than that of the type of *E. bielawskyi* and that of *C. johnstoni*. The lower carnassial is almost evenly proportioned in occlusal outline, except for a slight medial constriction between the protoconid and paraconid. The protoconid is higher than the paraconid. The metaconid is absent, and the talonid is unicuspid.

DISCUSSION

The genus *Chasmaporthetes*, type species *C. ossifragus*, was proposed by Hay, 1921, for a fragmentary, edentulous (roots only present) ramus from the Val Verde Mine, near Anita, Coconino County, Arizona. Stirton and Christian (1940) described a second ramus, with a complete dentition, from North Cita Canyon, Randall County, Texas, as the type specimen of *Ailuraena johnstoni* which they later (1941) transferred to *Chasmaporthetes*. The genus has until now been restricted to these two North American species, known only from rami, although later authors (Repenning, 1967; Savage and Curtis, 1970; Kurtén, 1971) have suggested synonymy with the European genus *Euryboas* Schaub, 1941.

Schaub (1941) described a mandible from Perrier-Rocca Neyra, France, as the type specimen of *Euryboas bielawskyi* and referred a partial maxilla with P^{3-4} from Val d'Arno, Italy, and several limb elements from these and other localities to this species. Schaub believed that *Euryboas bielawskyi* and *Chasmaporthetes johnstoni*, based on lower dentitions, were closely related but did not discuss *C. ossifragus*. Schaub also compared the partial maxilla of *E. bielawskyi* with the type specimen, a skull, of "*Lycyaena*" *lunensis* Del Campana, 1914, from Olivola (Val di Magra) Italy. Schaub (1941) noted the large parastyle and posteromedial position of the protocone on P^4, the long, thin premolars, and the larger anterior accessory cusps on the upper premolars of "*Lycyaena*" *lunensis*. Other than the shape of the premolars, which we use as a species character, the above features are also seen in the upper dentitions of *Chasmaporthetes kani* and are used in our revised generic diagnosis of *Chasmaporthetes*.

Viret (1954), with no large sample to aid his interpretation of variation, recognized the generic identity of *Euryboas*. He believed that the differences between "*Lycyaena*" *lunensis* and *Euryboas bielawskyi*, as discussed by Schaub (1941), and present in new material he described, could be nothing more than variation among individuals of different sizes and ages. Viret (1954) therefore synonymized *E. bielawskyi* with "*Lycyaena*" *lunensis* and referred a muzzle (QSV 53) from St. Vallier, a partial maxilla (University of Clermont no. 3285) from Senéze, and several isolated teeth possibly of the same individual (University of Clermont, unnumbered) from Perrier-Etouaires, to *Euryboas lunensis.*

The uniformity of characters in the sample of *Chasmaporthetes* from China and their similarity with "*Lycyaena*" *lunensis* Del Campana, in contrast to *Euryboas bielawskyi* Schaub, lead us to believe that Schaub (1941) was correct in separating "*Lycyaena*" *lunensis* and *Euryboas bielawskyi*. Furthermore, the similarity between the lower dentitions of *Chasmaporthetes kani* and

those of *C. johnstoni* and *C. ossifragus*, and between the upper dentitions and skulls of *C. kani* and "*Lycyaena*" *lunensis* indicate that these four species represent a discrete taxonomic unit which is separable from the original concept of *Euryboas* as proposed by Schaub (1941).

Of the specimens referred to "*Euryboas*" *lunensis* by Viret (1954), we would place one, the partial maxilla from Senéze, in *Chasmaporthetes.*[1] This partial maxilla has an alveolus for P^1, a large anterior accessory cusp on P^3, a large parastyle, and a posteromedially directed protocone of P^4, and a curved tooth row as is seen in *C. kani* and *C. lunensis.* The size of P^1, as indicated by the alveolus, and the length of P^3, relative to P^4, are less than is seen in either *C. kani* or *C. lunensis* and this specimen may not be referable to any described species of *Chasmaporthetes*.

The features of the lower dentition of *Chasmaporthetes kani*, which are also seen in *C. ossifragus* and *C. johnstoni*, in contrast to the type mandible of *Euryboas bielawskyi*, are the larger anterior accessory cusps on P_2-P_4, the more curved tooth row, and the slight imbrication of the premolars.

The lower premolars of *Chasmaporthetes kani* and *C. johnstoni* differ from those referred to *C. ossifragus* in having lower, less pointed, protoconids. The anterior accessory cusps on P_1 in both *C. kani* and *C. johnstoni* are less well developed than in P_1 of *C. ossifragus*. These are probably derived (apomorphic) characters of *C. ossifragus*. In *C. kani* and *C. ossifragus*, the lower premolars widen posteriorly; in P_3 and P_4 this widening is most evident in the appearance of a large posterior cingulum. In the lower premolars of *C. johnstoni*, the widest part of each tooth is near the central cusp. This more "cat-like" appearance is possibly a derived feature of *C. johnstoni*.

[1]Other specimens discussed by Viret (1954), a complete muzzle (QSV 53) from St. Vallier and several isolated teeth including P^3 and P^4, from Perrier, are referable to *Euryboas.* The muzzle lacks P^1, has straight tooth rows, the anterior accessory cusps on P^2 and P^3 are barely noticeable, and (as also seen in a P^4 from Perrier) the parastyle of P^4 is smaller than in *Chasmaporthetes* and the protocone is directed anteromedially and extends as far forward as the anterior margin of the tooth.

The size relationship of P_4 to M_1 quickly separates these three species of *Chasmaporthetes* and is probably a derived condition in both *C. johnstoni* and *C. ossifragus*. M_1 is only slightly larger than P_4 in *C. kani* (the presumed primitive condition also seen in *Lycyaena* and *Euryboas*) but much larger (nearly 25%, Klein, 1971) in *C. ossifragus* and slightly smaller than P_4 in *C. johnstoni* (Stirton and Christian, 1940).

The features of the type specimen of *Chasmaporthetes lunensis*, a skull and upper dentition, which are held in common with *C. kani* and in contrast to the maxillary fragment referred to *Euryboas bielawskyi* by Schaub (1941) and the muzzle and teeth referred to "*E.*" *lunensis, sensu lato,* by Viret (1954), are the presence of a large P^1, the larger parastyle and the position of the protocone on P^4, the slightly curved tooth row with the imbricate premolars, and the high, dorsally flattened muzzle. The shape of the muzzle is one of the more unusual features of *C. lunensis* in that the premaxillae rise above the level of the maxillae creating a saddle, or flat area, between the snout and the domed forehead. This may be due to crushing but is duplicated in the most complete skull of *C. kani*, F:AM 99783, and in complete contrast to the muzzle of *Euryboas*, as seen in QSV 53 from St. Vallier, in which the muzzle slopes smoothly upward from the premaxillae to the highly domed forehead. This may be a generic character of *Chasmaporthetes* but as it is questionable and can be examined in only three specimens, two of *Chasmaporthetes* and one of *Euryboas*, we have not included it in our revised generic diagnosis of *Chasmaporthetes*.

The upper dentition of *Chasmaporthetes kani* and *C. lunensis* differ in the size and shape of P^2 and P^3. In *C. lunensis* these teeth do not widen posteriorly and in *C. kani*, i.e., they lack large internal cingula, and they are relatively longer (the length of P^2 is about two-thirds that of P^4 and P^3 is about five-sevenths that of P^4, whereas in *C. kani* these proportions are one-half to three-fifths for P^2/P^4 and one-half for P^3/P^4). The external cingula on P^{2-4} of *C. lunensis* may be heavier than on *C. kani* but this is often individually variable among carnivores. Judging from the alveolus, P^1 of *C. lunensis* was about the same size as that of *C. kani*.

As *Chasmaporthetes ossifragus* and *C. johnstoni* are known from rami and lower dentitions

only and *C. lunensis* only from a skull, it is possible that *C. lunensis* is synonymous with one of the North American species. The large P^3, relative to P^4, of *C. lunensis* would lead one to expect a correspondingly large P_4, relative to M_1, as is seen in *C. johnstoni*. The lower premolars of *C. johnstoni* are also thin as are the upper premolars of *C. lunensis*. Only the discovery of additional material of either *C. lunensis* or *C. johnstoni* can verify this possible synonymy.

The type specimen of "*Hyaena*" *borissiaki* Khomenko, 1932, is an excellent partial skeleton from the Moldavian Republic, U.S.S.R. It agrees with our generic diagnosis of *Chasmaporthetes* in having a large P^1 (although smaller than in *C. kani* or *C. lunensis* and possible plesiomorphic), large accessory cusps on the premolars and in the position of the protocone on P^4. However, the lower tooth row is straight as in *Euryboas*, an apparent symplesiomorphy, and the snout is evenly sloping (also as in *Euryboas*) an apparent convergence. Although we have not examined the material, this species appears to be referable to *Chasmaporthetes sensu stricto*, in which it would be differentiated from the other species by the small size of M^1, the near equal lengths of P_4 and M_1, and the variable presence of P_1 (present on the right ramus of the type but not the left).

The occurrence of hyaenas in the New World has been regarded as a result of immigration from Asia over the Bering Isthmus (Hendey, 1975) sometime during the Late Tertiary, although as far as hyaenids are concerned direct evidence for this hypothesis was lacking. The Frick material fills a crucial gap in our understanding of this event, as it establishes a Holarctic distribution for *Chasmaporthetes* during the Early Pleistocene.

An interesting note on the distribution of hyaenas, and a possible African record of *Chasmaporthetes*, is "*Lycyaena*" *nitidula* Ewer, 1955 ("*L.*" *silberbergi nitidula* in Ewer, 1967), from the Swartkrans and Sterkfontein caves, South Africa. This species is certainly more correctly referable to either *Euryboas* (as De Beaumont, 1967, proposed) or *Chasmaporthetes* than to *Lycyaena* in that it has a deep mandibular symphysis, a large, single mental foramen on the ramus, and large anterior accessory cusps on P_{2-4} in contrast to the more doglike chin, two mental foramina, and much smaller accessory cusps of *Lycyaena*. P^2 and P^3 of "*Lycyaena*" *nitidula*, in fact, show a greater development of the anterior accessory cusps than is seen in known species of *Euryboas* or *Chasmaporthetes*. As *Chasmaporthetes* differs from *Euryboas* in having a greater development of the anterior accessory cusps, that genus may be the more correct reference. The large size of the parastyle and the placement of the protocone on P^4 support this referral although the recovery of additional material, which would illustrate the condition of P^1 and the degree of curvature of the tooth rows, would make this referral more certain.

REMARKS ON GENERIC RELATIONSHIPS

Simpson (1945) placed *Chasmaporthetes* in the Felidae, *incertae sedis*; a conclusion with which we disagree but which serves to introduce the taxonomic problems surrounding *Chasmaporthetes*. Various genera have been postulated as near relatives of *Chasmaporthetes*: *Ictitherium* (Hay, 1921), *Euryboas* (Kurtén, 1971), and *Percrocuta* (Hendey, 1975), although many authors (Savage and Curtis, 1970; Repenning, 1967) have tended to recognize the similarities between *Euryboas* and *Chasmaporthetes*. Hendey (1975) cited gaps in geographic distribution between these two genera and believed that the similarities between *Euryboas* Schaub, 1941, and *Chasmaporthetes* Hay, 1921, might be due only to convergence and not to close relationship. The discovery of *Chasmaporthetes* in China contradicts Hendey's (1975) hypothetical migration into North America of a species of *Percrocuta* Kretzoi, 1938, instead of *Euryboas*. *Chasmaporthetes* was apparently generically distinct before its entry into North America and shares a number of derived characters with *Euryboas* rather than with *Percrocuta*.[1]

[1]The taxonomic position of *Percrocuta* is uncertain although it is probably less closely related to advanced hyaenas than has been proposed (Hendey, 1975). *Percrocuta* appears to be an early parallel of the more advanced hyaenids. *Percrocuta* retains a number of primitive characters, such as a large metacarpal I (Hendey, 1974; metacarpal I is vestigial in all advanced hyaenids); yet is highly derived, even exceeding other hyaenids, in certain features such as reduction of the protocone of P^4; and has uniquely derived characters, such as a premaxillary-frontal contact in the skull, which are not seen in other hyaenids.

The taxonomic position of *Chasmaporthetes* as well as other generic relationships within the Hyaenidae can perhaps be most easily discussed and visualized in a cladistic framework (*sensu* Hennig, 1966; and Brundin, 1966). In a cladistic analysis, reduced to its most salient features, groups are considered to be naturally related (monophyletic) if they can be shown to share characters which are presumed to have newly arisen (are shared derived = synapomorphic) in their most recent, common, although hypothetical, ancestor from primitive character states. These monophyletic groups, supported by one or more synapomorphies, constitute testable hypotheses of a kind not generally provided by a phylogenetic "tree." Falsification can be provided by contradiction of homology or polarity of the characters utilized. As a principle of inquiry ". . . agreement in characters must be interpreted as synapomorphy as long as there are no grounds for suspecting origin to be symplesiomorphy (shared primitive) or convergence" (Hennig, 1965). The outcome is a display of relationships in which maximum parsimony is achieved, in that the greatest numbers of synapomorphic characters requiring the fewest parallel and convergent characters have determined the groupings. We chose to use a cladistic representation as it is clear, concise, and follows from a stated set of rules.

The hyaenids, exclusive of the problematical *Percrocuta* group, can be characterized as having (see figure 3, point 1):

(A) a large conical parastyle on P^4
(B) the protocone of P^4 placed directly lingual to the parastyle
(C) a broad posterior cingulum on P_4
(D) a short basicranium and a relatively elongate face
(E) a reduction of metacarpal I and metatarsal I
(F) long, slender, doglike limbs

Furthermore, the advanced genera of hyaenas, including the living species, form a phyletic group in that (branching point 2) they share:

(A) a high, triangular occipital crest
(B) long canines
(C) wide and robust premolars
(D) the absence of an entepicondylar foramen in the humerus
(E) frontal sinuses expanded posteriorly

The group which includes *Chasmaporthetes* as well as the modern hyaenids (branching point 3) is advanced with respect to its sister-group, containing *Palhyaena*, in having:

(A) deeper jaws
(B) reduced P_1 and M_2^2
(C) the palate broadened anteriorly
(D) P^1 crowded between C^1 and P^2
(E) an enlarged anterior mental foramen or absent posterior mental foramen

Chasmaporthetes, *Lycyaena*, and *Euryboas*, as recognized by De Beaumont (1967) in another phraseology, comprise a monophyletic group whose synapomorphic characters include (branching point 4):

(A) small or absent M_2^2 and P_1
(B) small or absent metaconid on M_1
(C) reduction of the labial portion of the posterior cingulum on P_4
(D) trenchant, catlike, premolars
(E) dental series in straight or only slightly curved rows

Chasmaporthetes is most closely related to *Euryboas* (together forming a natural group at branching point 5) in sharing:

(A) M_2^2 absent
(B) protocone of P^4 reduced
(C) I^3 slightly enlarged
(D) P_1 absent
(E) M_1 enlarged
(F) metaconid of M_1 absent
(G) talonid of M_1 unicuspid
(H) M^2 reduced
(I) a single, large mental foramen beneath P_2
(J) reduced angular process on the ramus

Chasmaporthetes differs from *Euryboas* in having (point 6):

(A) a high, long muzzle (plesiomorphic) as opposed to a shorter muzzle in *Euryboas* (apomorphic)
(B) P^1 enlarged (apomorphic) versus P^1 lost in *Euryboas* (also apomorphic)
(C) larger anterior accessory cusps on P_{2-4} (apomorphic)
(D) larger parastyle on P^4
(E) the protocone of P^4 is lingually directed and does not extend to the anterior limit of the tooth (apomorphic) as opposed to an anterolingually directed protocone in *Euryboas*,

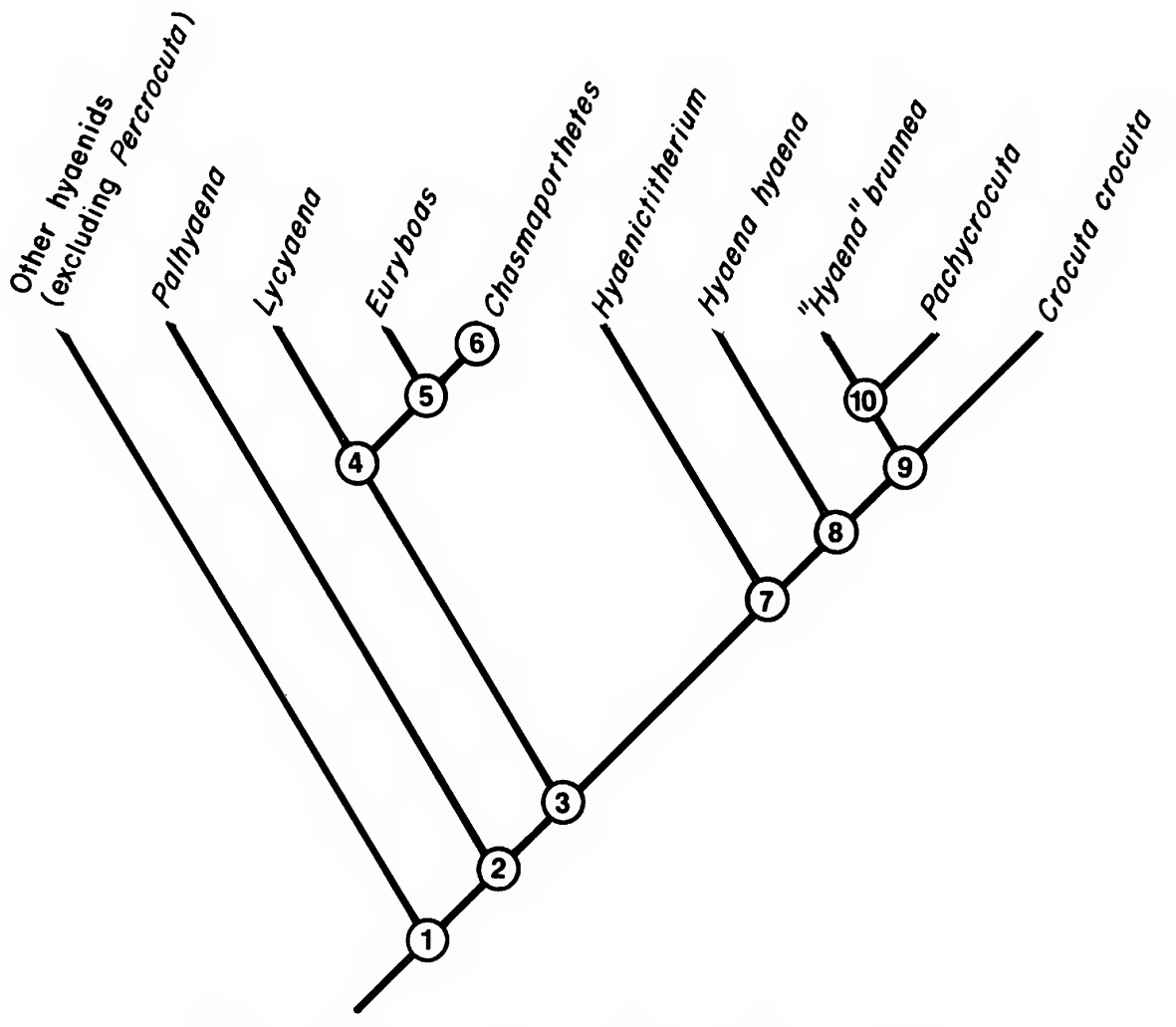

FIG. 3. A cladogram expressing the relationships of hyaenid genera.

which reaches as far forward as the anterior margin of P^4 (plesiomorphic)

(F) tooth rows curved with the premolars slightly imbricate, i.e., the posterior margin of a premolar sits labially to the anterior end of the following premolar (apomorphic).

The apomorphic features of the modern hyaenids and *Hyaenictitherium*[1] the sister group (branching point 7) to *Lycyaena*, *Euryboas*, and *Chasmaporthetes* are:

(A) enlarged I^3

(B) reduced P^1

(C) massive canines

(D) enlarged or swollen anterior cusp on P^3

Hyaena Brisson, 1762, *Pachycrocuta* Kretzoi, 1938, and *Crocuta* Kaup, 1828 (branching point 8), in relation to *Hyaenictitherium*, share: (A) the absence of P_1 and M_2^2, (B) reduced frontal sinuses, and, possibly, (C) shortened hind limbs. Lack of associated skeletal material for all genera prevents certain recognition of the last character.

One of the more interesting observations in this expression of relationships is that the brown hyaena, "*Hyaena*" *brunnea*, is more closely re-

[1]In the use of *Hyaenictitherium* Kretzoi 1938, type species *H.* ("*Ictitherium*") *hyenoides* Zdansky 1924, we differ in opinion from Ficcarelli and Torre, 1970, who would retain this species in *Ictitherium*.

TABLE 2
Some Morphological Comparisons of Hyaenid Genera

	Palhyaena	*Lycyaena*	*Euryboas*	*Chasmaporthetes*
Palate	Long and narrow	Long and slightly broad	Short and broad	Long and broad
I^3	Small	Small	Slightly enlarged	Slightly enlarged, large in North American forms
P^1	Small	Small	Absent	Very large
P^2	Long and slender	Long and slender	Long and slender	Long and slender
P^3	Long and slender	Long and slender, faint anterior cusp	Slightly reduced in length, faint anterior cusp	Long and slender, prominent anterior cusp
M^1	Small	Very small	Smaller than *Lycyaena*	About the same size as in *Euryboas*
M^2	Small	Very small when present	Absent	Absent
Mandible	Long and slender	Long and slender, mental foramen beneath P_2 large	Long and deep, a single large mental foramen beneath P_2	Same as in *Euryboas*
P_1	Small	Very small, sometimes absent	Absent	Absent (except in *C. borissiaki*)
P_2	Long and slender	Long and slender	Short and slightly robust	Long and slender with small anterior cusp
P_3	Long and slender	Long and slender	Long and slender, slightly more robust than in *Lycyaena*	Long and slender, anterior cusp present
P_4	Strong lingual cingulum, faint anterior cusp	Lingual cingulum reduced, anterior and posterior cusps prominent	Same as in *Lycyaena*	Lingual cingulum reduced, anterior and posterior cusps prominent
M_1	Metaconid reduced, talonid small and bicuspid	Metaconid very small, talonid very small and bicuspid	Metaconid absent, talonid unicuspid and trenchant	Metaconid absent, talonid unicuspid and trenchant
M_2	Small	Absent	Absent	Absent

lated to *Pachycrocuta* and *Crocuta* than to *Hyaena hyaena*. Although superficially very similar in appearance, and sharing a number of plesiomorphic features such as having a metaconid and bicuspid talonid on M_1, the striped and brown hyaenas apparently do not form a natural group. The apomorphic features that "*Hyaena*" *brunnea* shares with *Pachycrocuta* and *Crocuta* (branching point 9) are:

(A) large conical P^3's

(B) the anterior cusp of P^3 formed into a ridge

(C) talonid of M_1 small and metaconid of M_1 reduced or absent

Furthermore, "*Hyaena*" *brunnea* and *Pachycrocuta* (branching point 10) each have a larger P_2, deeper jaws, and less reduced M^1 than does *Crocuta*.

A comparison of some morphological characters of *Chasmaporthetes* and other hyaenid genera is given in table 2.

TABLE 2 – (*Continued*)

Hyaenictitherium	*Hyaena hyaena*	*"Hyaena" brunnea*	*Pachycrocuta*	*Crocuta*
Long and slightly broad	Long and slightly broad	Short and broad	Very short and broad	Very short and broad
Slightly reduced	Large and robust	Large and robust	Large and very robust	Large and robust
Slightly reduced	Small and rounded	Small and rounded	Small and rounded	Small and rounded
Small and slender	Small and slender, strong anterior cusp	Small and robust	Small and robust	Very small and robust
Robust with enlarged anterior cusp	Robust with very enlarged anterior cusp	Large and conical	Large and conical	Very large and conical
Slightly reduced when compared with *Palhyaena*	Small	Smaller than in *H. hyaena*	Very small	Very small when present
Very small	Absent	Absent	Absent	Absent
Variable, but never very deep, mental foramen beneath P_2 large	Long and deeper than in *Hyaenictitherium*, a single large foramen beneath P_2	Short and deep, a single large mental foramen beneath P_2	Same as in *"H." brunnea*	Short and shallow, a single large mental foramen beneath P_2
Very small, sometimes absent	Absent	Absent	Absent	Absent
Small and slender	Small, strong anterior cusp	Short and robust	Short and robust	Very short and robust
Short and slightly robust	Robust with prominent anterior cusp	Large and conical	Large and conical	Very large and conical
Small lingual cingulum cusp sometimes present, anterior posterior cusps prominent	Lingual cingulum cusp present, weak posterior cusp and strong anterior cusp	Large and very robust	Large and very robust	Small and slender
Same as in *Palhyaena*, but larger	Small, talonid reduced and bicuspid	Large, metaconid and talonid small, talonid bicuspid	Large, metaconid rarely present, talonid sometimes unicuspid	Very large, metaconid absent, talonid unicuspid
Very small	Absent	Absent	Absent	Absent

ECOLOGICAL ROLES

The ecological equivalency of the borophagine dogs in the New World with the Old World hyaenids is a well-known relationship (see for example Romer, 1966, and Kurtén, 1971). The comparison of roles is, however, usually confined to the more characteristic members of each group, *Crocuta* and *Borophagus*, and overlooks an almost parallel evolutionary history of the two groups. For example, the characteristic and typically nonhyaenid features of *Chasmaporthetes* can also be seen in the borophagine *Aelurodon taxoides* group of McGrew (1944). The premolars of both genera form nearly straight rows, have strong anterior and posterior cusps, and are long and thin. P^1 of each is exceptionally large within each subfamily. The metaconid of M_1 is reduced or absent; the talonid is unicuspid or nearly so in each genus. Both genera have well-developed jaws with heavy chins.

Whereas *Chasmaporthetes* and *Aelurodon taxoides* lengthen and strengthen the premolars and premolar area of their jaws, *Crocuta* and *Borophagus* have reduced the anterior premolars and developed a large, conical piercing tooth. *Chasmaporthetes* and *Aelurodon taxoides* may have been occupying the ecological role now filled by wolves and hunting-dogs (*Lycaon*).

Other ecological equivalencies between genera of borophagine dogs and *Tomarctus* and hyaenids are given in table 3.

SUMMARY AND CONCLUSIONS

Chasmaporthetes kani, new species, from deposits of Nihowanian age (Early Pleistocene) in Shansi Province, People's Republic of China, is the first member of this genus found in Asia and the first species for which both upper and lower dentitions are known. "*Lycyaena*" *lunensis* (Del Campana, 1914), known from the holotype skull only, from the Villafranchian Val d'Arno of Italy, is transferred to *Chasmaporthetes* as its affinities with the North American late Blancan and Irvingtonian species, *C. ossifragus* Hay, 1921, and *C. johnstoni* (Stirton and Christian, 1940), can now be recognized. *Euryboas bielawskyi* Schaub, 1941, is the Villafranchian type species of *Euryboas*.

Chasmaporthetes is apparently most closely related to *Euryboas*. *Chasmaporthetes*, *Euryboas*, and *Lycyaena* form a natural group in sister-group relationship to *Hyaenictitherium*, *Hyaena*, *Pachycrocuta*, and *Crocuta*.

Among the Pliocene and Pleistocene hyaenids there were apparently two major adaptive trends. One, the *Chasmaporthetes* group, had more elongate premolars, straighter tooth rows, a strong chin, and no development of bone-splitting premolars. The second, in which all modern hyaenas and *Hyaenictitherium* are included, was a bone-crushing habitus involving the acquisition of heavy premolars and a short, wide skull concomitant with a curved tooth row, including a large conical piercing tooth, P_4, in *Pachycrocuta* and *Crocuta*. Theoretically, these conditions could have developed independently a number of times within hyaenid genera. However, in identifying these adaptations and hypothesizing that they are the result of major adaptive shifts in only two lines of hyaenas, we are assuming that the presence of these characters in a hyaenid genus results from direct inheritance and demonstrates its inclusion within a monophyletic group. These character suites are derived characters at branching points 4 and 7 in our cladogram (fig. 3) and become primitive characters at lower taxonomic levels. Other derived characters, not specifically related to either of these trends, such as the loss

TABLE 3

Morphological and Ecological Equivalencies between Genera of the Hyaenidae and Borophaginae

Hyaenidae	Borophaginae	Morphological Features	Role
Crocuta	*Borophagus–Osteoborus*	Short-faced, large conical piercing tooth, reduced anterior premolars, horizontal ramus shallow	"Spotted hyaena" bone-crushing carnivore
Pachycrocuta brevirostris	*Aelurodon haydeni*	Large, short-faced, massive dentition, horizontal ramus deep	"Large spotted hyaena" large bone-crushing carnivore
Lycyaena-Euryboas-Chasmaporthetes	*Aelurodon taxoides* group-*Strobodon*	Long-faced, P^1 large, premolars trenchant, horizontal ramus deep	"Large hunting dog" strong-jawed (grasping) carnivore
Palhyaena	*Tomarctus*	Long muzzle, slender rami, unmodified premolars, unreduced metaconid and talonid on M_1	"Jackal-coyote" generalized canoid form

of M^2, M_2, and P_1, are then assumed to be characters occurring in parallel at branching points 5 and 8 rather than indicative of relationship between the *Crocuta* group (exclusive of *Hyaenictitherium*) and the *Chasmaporthetes* group (exclusive of *Lycyaena*).

The Plio-Pleistocene evolution of Old World hyaenids paralleled the Mio-Pliocene history of borophagine canids in the New World. From an early, undifferentiated stock of small, unspecialized, doglike carnivores, two major trends developed in both groups. One, which included *Chasmaporthetes* in the Hyaenidae and *Aeluroden taxoides* in the Borophaginae, expanded the doglike habitus, and probably filled the role of the wolf or hunting-dog of today. The second, in which are included living hyaenas and *Borophagus* itself, developed heavy premolars and brachycephalic skulls associated with the bone-crushing habitus of modern hyaenas.

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